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*THE 'HOMING HABITS' OF THE PULMONATE MOLLUSK
ONCHIDIUM¹*

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For some time it has been known that the limpets and their allies living on shore rocks exposed by the falling tide exhibit the habit of returning, on the approach of the period of low water, to particular spots where they have individually made 'homes,' slight depressions in the rock-surface, which usually fit with considerable exactness the form and irregularities of the limpet's shell. From this 'home' the limpet may creep away 50 to 90 cm., when covered by the sea, to feed—frequently following well-defined paths, to which it also adheres when creeping homeward again. Such experimental work as has been directed to the study of this peculiarity has gone to show that it may be regarded as depending upon tactile and perhaps other forms of irritability (Bohn, Piéron), the mollusk remembering (possibly) a sensory map of the topography of its home region. It cannot be said, however, that this matter is as yet thoroughly understood. 'Homing' behavior of a similar sort has also at various times been attributed, in an anecdotal way, to different terrestrial slugs and snails.

It seems previously to have escaped attention that homing movements of a more striking character are to be found in another gastropod, the intertidal naked pulmonate *Onchidium*. We have studied in this respect the behavior of *Onchidium* (*Onchidella*) *floridanum* Dall, and although further investigation of the subject has been planned, it is thought well to record here the nature of certain of our findings.²

The homing phenomenon to which we refer may be characterized as follows: *Onchidium* lives in groups, or communities, numbering up to a dozen or more individuals in each, which during high tide find shelter in cavities within the eroded shore rock; these cavities are either narrow crevices, or may be sub-spherical with a diameter as great as 6 cm.; but in any case they communicate with the exterior by means of a small and almost undetectable opening

(usually single), commonly obstructed by the growth of small mussels (*Modiolus*). When, during daylight hours, the tide has fallen to such an extent that an *Onchidium* 'nest' has been above water-level for about half an hour, which frequently happens about two hours before extreme low tide (but, for many nests, does not occur at all during neap tides), the *Onchidia* in that nest creep out, in succession, wander some distance over the algae-covered rocks, on which they feed, and then (at least an hour before their nest would again be covered by the rising of the tide) all return to that nest. The period of exposure lasts about two hours. Any one community may include individuals of varying lengths up to 2 cm.

The *Onchidia* return each to its own particular nest, even on much-eroded rocks and where the nests are many and close together, and that in spite of the fact that the individuals emanating from different nests frequently mingle during their wanderings. The snails comprising anyone community begin the return to their nest almost simultaneously, although they may be scattered over an area a meter in diameter and may be situated on opposite sides of the nest.

Clearly, at least two distinct problems are presented by this behavior: First, why do the *Onchidia* return to the nest, and above all, why do the various members of a group begin almost simultaneously to make this return? Secondly, what is the nature of the directive control of the return journey itself? For the present, we discuss only the latter problem.

Onchidia situated at some distance from their nest pursue a fairly direct path toward it when they begin to return; previously, their paths may have been quite irregular. One or more approximately linear depressions may be adhered to in the immediate vicinity of the nest itself, but this is not necessary. An individual taken from one side of its nest, and placed on the opposite side, at a distance of a meter or slightly more, frequently, exhibits little or no hesitation in turning and moving directly toward the nest.

The possibility of vision of the entrance to the nest, of heliotropic orientation, or of wind influence, severally or in combination, can be perfectly excluded from the rôle of directive agents in this matter. Neither can the wetness nor dryness of the substratum or of the animals' tissues be important, for the behavior of the snails is the same during a dry and torrid afternoon as in a drenching down-pour of rain.

In an intensively studied situation where a number of *Onchidium* nests were found close together (30 to 50 cm. apart), it was seen that an *Onchidium* of one community so placed as to creep across the tiny sunken gully followed by the members of a neighboring colony would sometimes after hesitation, take this path and follow it for some centimeters; but in only one out of ten such instances did it actually *enter* the foreign nest; always there was hesitation and a retracing of the path, combined in several cases with an encircling journey about the foreign entrance. Yet, neither on the natural surfaces which they frequent, nor on various artificial surfaces tested does an *Onchidium* evince

any tendency to follow its own slime-track or that of another individual; nor does it 'favor' a wet or a dry surface, a rough or a smooth one, in any detectable way (as, for example, an earthworm does).

It may be considered that some form of contact irritability, perhaps resident in the oral lapets, is partially responsible for this behavior. Experimental tests of this point, which are difficult to secure, are not yet complete. If the path ordinarily followed in the immediate vicinity of the nest be scraped bare, or the rock at the very entrance to the nest be chiseled away, the *Onchidia* endeavoring to return there collect at the edge of the cleaned area and then wander about in its neighborhood until they are covered by the tide (and washed off the rock).

There are additional features, of the first importance: An *Onchidium* found returning to its nest may be carried 50 cm. away and placed on rock above high water level, where these animals never go naturally, and in at least half the trials the snail succeeds in getting back to its nest. If a nest to which the inmates have returned be broken open and the animals placed on the rock at distances up to 50 cm. from the former entrance, they have no serious difficulty in making their way to the location of the old home.³ *Onchidia* from neighboring colonies, or from laboratory stock, make no attempt to enter such a nest.

We are therefore forced to the provisional opinion that an *Onchidium* returns to its particular nest by virtue of some internal condition, simulating memory of the position of this nest in terms of its surroundings, but independently of the guidance which may be afforded by mechanically directive features of the environment.

To the extent that the homing movements of *Onchidium* may be proved to involve associative memory, this snail may be placed in a series comprising such types as *Chiton*, *Fisurella*, *Onchidium*, and *Octopus*, all four of which, in a sense, exhibit homing behavior, but of increasing degrees of precision and complexity in the order of the arrangement here given. The further study of *Onchidium*, both for itself and in relation to these other mollusks, should give rise to some valuable conclusions.

Summary.—*Onchidium floridanum* lives during high tide in 'nests,' cavities in the rock containing a number of individuals, from which the mollusks at low water emerge to feed upon exposed shore surfaces. The individuals emanating from any one nest return simultaneously to that nest before the tide rises again, and during this return give evidence of homing behavior, which seems to depend mainly upon internal conditions akin to the remembrance of specific localities.

¹ Contributions from the Bermuda Biological Station for Research, No. 95.

² A more complete account of these observations, with supplementary material, will be found in our paper, 'On the behavior of *Onchidium*,' shortly appearing elsewhere.

³ When a nest has two openings, the removed inmates, or some of them, may turn directly to the *second* opening and enter there, even if they have in the first instance employed the other entrance.